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- FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.
- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.
- THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

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A REVISION OF
THE ORNITHISCHIAN DINOSAUR
KANGNASAURUS COETZEEI HAUGHTON,
WITH A CLASSIFICATION OF
THE ORNITHISCHIA

By

MICHAEL R. COOPER

Cape Town

Kaapstad

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A REVISION OF THE ORNITHISCHIAN DINOSAUR *KANGNASAURUS COETZEEI* HAUGHTON, WITH A CLASSIFICATION OF THE ORNITHISCHIA

By

MICHAEL R. COOPER

*National Museum, Bulawayo, Zimbabwe**

(With 22 figures)

[MS accepted 11 July 1984]

ABSTRACT

The osteology of *Kangnasaurus coetzeei* Haughton is redescribed on the basis of the hypodigm, and figured in detail. Long considered an iguanodontid, it is here shown to be most closely allied to *Dryosaurus* and is thus transferred to the Hypsilophodontidae. To judge from its evolutionary grade, the early Cretaceous age assigned to *Kangnasaurus* seems reasonable. The unsatisfactory higher taxonomy of the Ornithischia, in particular the Ornithopoda, has resulted in a cladistical analysis of the group and the introduction of a new classification.

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INTRODUCTION

The occurrence of dinosaur bones at the base of the Kalahari succession in the northern Cape (Fig. 1) was reported by Rogers (1915), and the find was described by Haughton (1915). The material was obtained from a poorly sorted, immature, coarse clastic unit of colluvial rubble exposed in a well at a depth of approximately 34 m. Although there are preservational differences amongst some of the bones all the femora are undoubtedly conspecific while most of the other bones are certainly of ornithopod character. Furthermore, there is no reason to believe that the femora belong any more certainly with the holotype tooth than do the highly porous dorsal and caudal vertebrae. These preservational differences are here related to postdepositional differential leaching and the entire collection of dinosaur bones from this well is treated as the hypodigm of *Kangnasaurus coetzeei* Haughton. The writer is of the belief that when dealing

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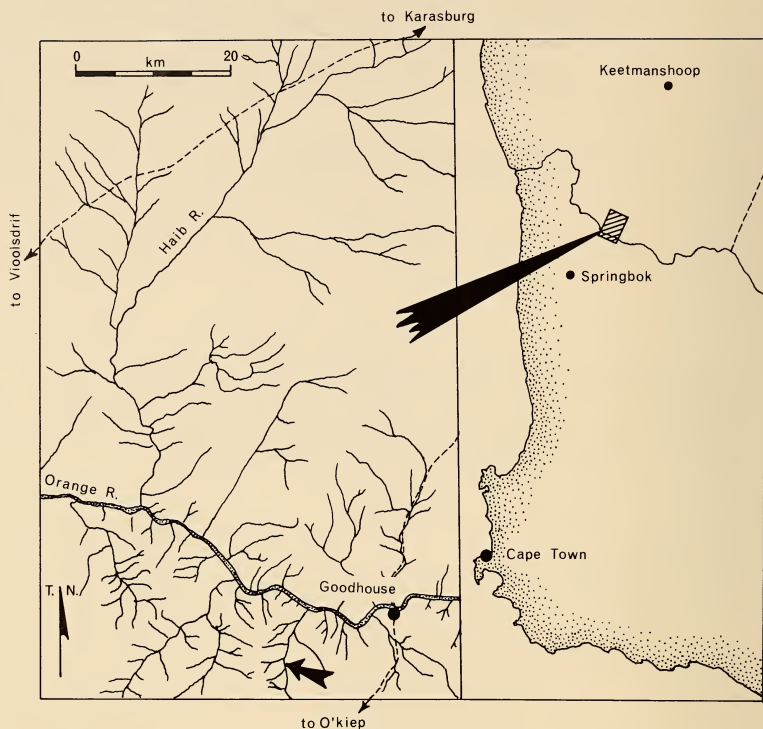


Fig. 1. Locality map with fossil site arrowed.

with such disarticulated remains there is a high degree of probability that all the bones are from individuals of the same taxon. Since, however, this probability cannot be quantified, the burden of proof must lie with the dissenter to establish conclusively that more than one taxon is involved. Thus, Steel's (1969: 19) statement (taken almost verbatim from Haughton (1915: 259)) that '... the foot bones and vertebrae appear to come from a different deposit to the type and their inclusion in this genus is questionable' is here rejected. The preservation of the foot bones and tibiae are identical to those of the femora.

It is clear from the literature that *Kangnasaurus* is a poorly known genus, yet the available material allows for a better understanding of the taxon than provided by Haughton (1915). Consequently, it is the purpose of this paper to

redescribe and illustrate the available material of *K. coetzeei*, and to show that its affinities have been misinterpreted previously.

All the material is housed in the palaeontological collections of the South African Museum under the catalogue numbers SAM-2731 and SAM-2732.

ORNITHISCHIAN TAXONOMY

Present classification of the Ornithischia, in particular the Ornithopoda, is unsatisfactory (Maryńska & Osmólska 1974; Santa Luca 1979; Dodson 1980; Coombs 1982), while earlier classifications (Thulborn 1971, 1975; Galton 1972) recognized horizontal 'grades' rather than monophyletic lineages. Since the writer follows Santa Luca (1979) in regarding the presence or absence of an obturator process to the ischium as of prime taxonomic importance, a new classification of the Ornithischia is proposed (Fig. 2). This is based upon the following character suites:

Character suite A

Subclass DINOSAURIA Bakker, 1975

Archosaurs with a wide open iliac acetabulum, prominent 4th trochanter, mesotarsal ankle and ascending process to the astragalus. Pubis long, thickened distally.

Character suite B

Cohort CARNOSAURIFORMES new cohort

Dinosaurs retaining the primitive condition of recurved thecodontian dentition with finely serrated cutting edges.

Character suite C

Cohort ORNITHISCHIFORMES new cohort

Dinosaurs with laterally compressed, leaf-shaped teeth bearing marginal denticles to the cutting edge. Dentition heterodont with non-recessed, marginal cheek teeth.

Character suite D

Superorder PACHYPODOSAURIA new superorder

Long-necked ornithischiforms that retain the primitive brachyiliac pelvis.

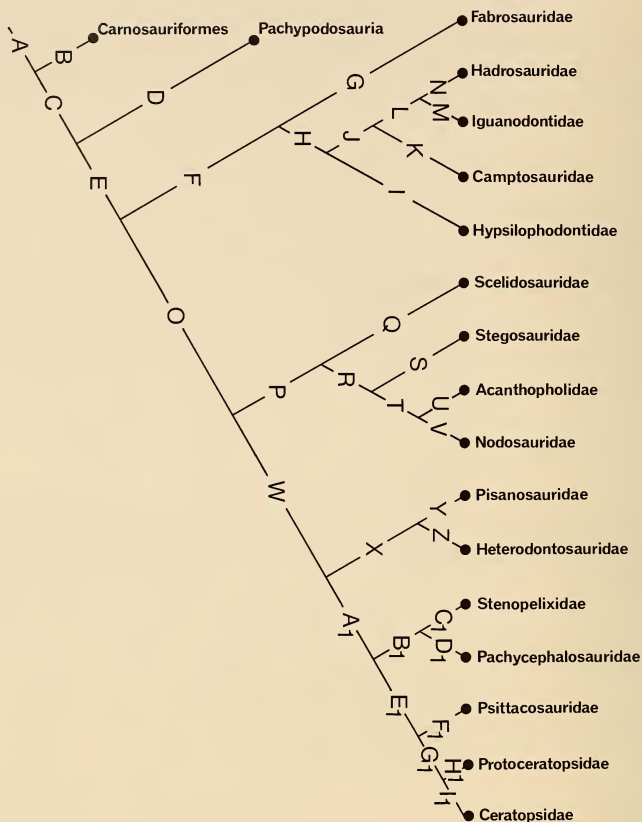


Fig. 2. Hypothesized relationships amongst the Ornithischia.

Character suite E

Superorder ORNITHISCHIA Seeley, 1888 (nom. transl. herein
ex order Ornithischia)

Herbivorous ornithischiforms with wear facets to the cheek teeth, an opisthopubic pelvis, a supraorbital element, a predentary bone to the mandible, an inturned head to the femur, and a pendent 4th trochanter.

Character suite F

Order ORNITHOPODA Marsh, 1871 (nom. transl. herein
ex suborder Ornithopoda)

Ornithischians with an obturator process to the ischium, at least 24 pre-sacra, a jugal of normal size that lacks a prominent ventral flange, and a prominently flared lesser trochanter separated by a deep cleft from the femoral shaft.

Character suite G

Suborder FABROSAURIA new suborder

Ornithopods retaining the primitive condition of non-recessed, marginal cheek teeth. Lateral surface of maxilla flat, dentary slender. Jaw articulation in line with tooth row. Six premaxillary teeth. Cheek teeth lack well-defined occlusal wear surfaces. Prepubis short.

Superfamily FABROSAUROIDEA new superfamily

Diagnosis as for suborder.

Family NANOSAURIDAE Marsh, 1878

Diagnosis as for suborder. Since Galton (1978) includes *Nanosaurus* within the Fabrosauridae, the latter taxon (Galton 1972) is a junior subjective synonym of the family Nanosauridae.

Character suite H

Suborder HYSILOPHODONTIA new suborder

Ornithopods with recessed cheek teeth roofed by an overhanging maxilla and floored by a massive dentary. Cheek teeth markedly asymmetrical, with prominent ridging of opposing surfaces. Jaw articulation ventrally offset. Elevated coronoid process and well-developed retroarticular process. Prepubis long.

Character suite I

Superfamily HYSILOPHODONTOIDEA new superfamily

Hysilophodonts retaining the primitive ornithopod characters of a short, high skull with large orbits, premaxillary teeth, small external nares, moderately developed antorbital vacuities and dermal armour. Diastema separating premaxillary teeth from those in the maxilla. Horny beak anteriorly. Maxillary teeth lack median ridge, but medial surface of dentary teeth strongly ridged. Posterior cervicals and dorsal vertebrae amphicoelous. Scapula short, expanded distally. Anterior intercondylar groove to femur weakly developed or absent.

Family HYPHILOPHODONTIDAE Dollo, 1882

Diagnosis as for superfamily.

Character suite J

Infraorder IGUANODONTIA Dollo, 1888

Large to very large graviportal hypsilophodonts. Head large, long, laterally compressed, with elongate snout, vestigial antorbital vacuities, and large external nares. Premaxilla edentulous, separating maxilla from nasal. Nasals elongate. Teeth unilaterally enamelled, those of the maxilla with a median ridge. Cervical and anterior dorsal vertebrae opisthocoelous. Scapula long, straight, slender. Humerus relatively narrow, with weak deltopectoral crest. Posterior process of ilium relatively produced and somewhat decurved, with brevis shelf. Pubis and ischium decurved. Carpus compact, generally well ossified. Digit III of manus with three phalanges. Pedal digit I reduced. Astragalus lacks an ascending process.

Character suite K

Superfamily CAMPTOSAURIOIDEA new superfamily

Primitive iguanodonts retaining a single supraorbital and curved femur with shallow anterior intercondylar groove. Premaxilla expanded, almost encircling nares. Quadrate short, curved, inclined. Short ventrolaterally directed basipterygoid processes. Phalangeal formula for manus 2-3-3-3-2. Prepubis relatively shallow, postpubis as long as ischium.

Family CAMPTOSAURIDAE Marsh, 1888

Diagnosis as for superfamily.

Character suite L

Superfamily IGUANODONTOIDEA Hay, 1902

Iguanodonts with digit I of the manus reduced; digit III with a 'hoof-like' ungual. Prepubis relatively deep; postpubis reduced, shorter than ischium. There are 5-8 sacral vertebrae. Femur straight, columnar, with very deep anterior intercondylar groove. Pedal phalangeal formula 0-3-4-5-0.

Character suite M

Family IGUANODONTIDAE Cope, 1896

Iguanodontoids with a low skull, two supraorbital elements and a slender coronoid process. Phalangeal formula of manus 1-3-3-3-4, with a spur-like phalanx to the pollex. There are 5-6 sacral vertebrae.

Character suite N

Family HADROSAURIDAE Cope, 1896

Specialized aquatic iguanodontoids with expanded premaxillaries forming a duck-like bill. Premaxillae and nasals frequently extensively modified, sometimes forming a crest. Supraorbital elements lacking. Maxillae and mandibular rami with dental battery comprising 45–60 rows of successional teeth. There are 30–34 presacra (approximately 15 cervicals) and usually 8 sacral vertebrae. Ilium with antitrochanter. Ischium straight. Femur with enclosed anterior intercondylar groove. Pollex absent; phalangeal formula of manus 0–3–3–3.

Character suite O

Order NEORNITHISCHIA new order

Ornithischians lacking an obturator process to the ischium and with recessed cheek teeth. Humerus with expanded head and prominent deltopectoral crest. Ulna with distinct olecranon.

The presence of recessed cheek teeth in the neornithischians is a character shared with hypsilophodonts. As noted by Galton (1973), cheek pouches merely reflect advanced adaptation to herbivory and hence may have evolved more than once, in different herbivorous lines. The fact that they are present in the early Carnian *Pisanosaurus* but absent in the Hettangian *Fabrosaurus* supports a fundamental dichotomy within the Ornithischia.

Character suite P

Suborder THYREOPHORINA Nopsca, 1915

Large to very large, heavily armoured, quadrupedal neornithischians with edentulous premaxillae and vestigial to absent antorbital vacuities. The cheek teeth reflect the primitive condition and are laterally compressed, deeply denticulate and feebly developed. External nares subterminal and laterally directed. Skull relatively low and long.

Character suite Q

Infraorder SCALIDOSAURIA new infraorder

Very primitive thyreophorinids, which are relatively weakly armoured compared to the remainder of the group, with four sacral vertebrae, reduced upper temporal fenestrae and ossified axial tendons.

Retains such primitive ornithischiform characters as a supra-acetabular buttress to the ilium, maxillary teeth that close outside those of the dentary (in prosauropod fashion), the lack of wear facets to the teeth, two distal tarsals, moderately long spool-shaped amphicoelous cervical vertebrae, distal condyles to femur with practically straight lateral margin and expanded medial condyle, limb

bones comparatively slender with main elements hollow, tibia shorter than femur, humerus 70 per cent of femoral length, hind foot functionally tridactylous, the hallux reduced and digit V apparently lacking, and with a pedal phalangeal formula of 2-3-4-5-0. The number of presacral vertebrae is uncertain; there are 17 dorsals and at least 6 cervicals; perhaps there were 25 presacrals as in the prosauropods.

There are still considerable problems surrounding *Scelidosaurus* and it is seriously in need of modern revision. One of the major sources of controversy surrounds the status of the 'juvenile *Scelidosaurus*' (Charig 1972; Galton 1975; Thulborn 1977), which Thulborn believes to be generically distinct and allied to *Fabrosaurus*. It differs from the adult holotype in having a very short prepubis, which led Romer (1968) and Galton (1975) to conclude that it was a primitive ankylosaur, while Charig (1976) has commented on its 'ankylosaur-like' skull. However, a short prepubis is primitive for the ornithischians since it is also found in *Fabrosaurus* and *Heterodontosaurus*. Thulborn (1977) also pointed to the fact that the postpubis of the juvenile was as long as the ischium whereas that of the adult was shorter. It is to be wondered whether these differences are not the result of allometric growth, with juveniles reflecting the primitive condition (as has been suggested for the prosauropod *Euskelosaurus*, cf. Cooper 1981).

Zittel (1932), Romer (1956) and Steel (1969) have all treated *Scelidosaurus* as a monotypic subfamily within the Stegosauridae. It is, however, so primitive, and thus resembling ornithopods, that it should certainly be housed in its own family.

Thulborn (1977) regarded the juvenile *Scelidosaurus* as closely allied to *Fabrosaurus*, but its short prepubis and the lack of an obturator process suggest it is at least as close to *Heterodontosaurus*. In addition, the femoral head of *Scelidosaurus* is said to be subglobular, perhaps reflecting poor discrimination between the femoral head and greater trochanter, as found in *Heterodontosaurus*. The two genera also have a brevis shelf to the ilium, while the supraorbital of *Scelidosaurus* was said to resemble that of *Stegoceras* (Coombs 1972).

Family SCELIDOSAURIDAE Cope, 1869

Diagnosis as for infraorder.

Character suite R

Infraorder STEGOSAURIDAE new infraorder

Thyreophorinids in which the jugal is small, the quadrate inclined and the upper temporal fenestrae are reduced to absent. External nares moderately large. Retroarticular and coronoid processes poorly developed to absent. Neck short, with abbreviated, disc-like centra. Vertebrae platycoelous to amphiplatyan. Transverse processes of dorsal vertebrae inclined upwards. Ilium with long anterior and short posterior process. Limb bones solid, or nearly so. Cnemial

crest of tibia poorly developed. The 4th trochanter is represented by a rugosity only. Ungual phalanges of pes 'hoof-like'.

Character suite S

Superfamily STEGOSAUROIDEA Marsh, 1877 (nom. transl. herein
ex suborder Stegosauria)

Stegosauiromorphs with a proportionately very small skull and three supraorbital elements. Neural arches and spines of posterior dorsals, sacrals and anterior caudals very tall. Sacral cavity greatly enlarged. Femur columnar with small lesser trochanter and little distinction between the femoral head and greater trochanter. About 27 presacrals (10 + 17). Ilium with decurved anterior process. Humerus less than half femoral length. Ventral end of scapula greatly expanded. Astragalus and calcaneum may fuse with each other and with epipodials. Metapodials very short. Phalangeal formula of pes 0-3-3-0. Dermal armour very prominent, comprising large vertical plates and long spines.

Character suite T

Superfamily ANKYLOSAUROIDEA von Huene, 1914 (nom. correct. Osborn, 1923;
nom. transl. herein ex suborder Ankylosauria)

Stegosauiromorphs characterized by the massive development of dermal armour, with skull partially or largely covered by dermal ossifications. Upper temporal fenestra closed. Lateral temporal fenestra strongly reduced, slit-like, or occluded by armour. Orbits small, with overhanging supraorbital region. There are 6-9 sacrals. Anterior process of ilium out-turned to a marked degree. Pubis greatly reduced; no prepubis and postpubis rudimentary. Ischium strongly curved distally. Caudal vertebrae short.

Character suite U

Family ACANTHOPHOLIDAE Nopsca, 1902

Moderately sized, primitive ankylosaurs with thin accessory dermal covering to the skull and only moderately developed dermal armour.

Character suite V

Family NODOSAURIDAE Marsh, 1890

Large to very large ankylosaurs with a comparatively large skull displaying a short, rounded snout and broad posterior margin. The jugal is deeply sculptured. A thick dermal covering is present, comprising separately ossified plates of varying sizes. Atlas-axis usually fused while the dorsal ribs are frequently co-ossified with the vertebrae. Anterior process of ilium broad. Acetabulum sometimes closed. Femur massive. Armour very heavy, encasing the tail, and in the pelvic region frequently fusing with the ilia, vertebrae and ribs.

Character suite W

Suborder NEORNITHOPODA new suborder

Neornithischians with subcylindrical cheek teeth displaying planar wear surfaces. Jugal with prominent ventral flange. There are 21–22 presacral vertebrae.

Character suite X

Infraorder HETERODONTOSAURIA new infraorder

Primitive neornithopods retaining a small skull with large orbits, well-developed antorbital vacuities, and small external nares. Greater trochanter poorly distinguished from femoral head. Lesser trochanter small, adpressed to femoral shaft.

Character suite Y

Family PISANOSAURIDAE Casamiquela, 1967

Very primitive heterodontosaurs with an unfused ankle resembling the prosauropod condition. Cheek teeth apparently unridged (due to wear, according to Bonaparte 1976). Coronoid process prominent. Retroarticular process moderately developed. Femur with prominent posterior intercondylar groove. Dentary massive, much of it lateral to tooth row.

Character suite Z

Family HETERODONTOSAURIDAE Romer, 1966; Kuhn, 1966

Heterodontosaurs with caniniform processes to the premaxilla and dentary. Nasals bulbous. Prepubis short, deep; postpubis long. Femur lacking anterior and posterior intercondylar grooves. Tibia–fibula and astragalus–calcaneum fused to form functional tibiotarsus and tarsometatarsus respectively. Three distal tarsals. Cheek teeth prominently ridged.

Character suite A₁

Neornithopods in which the antorbital vacuity is vestigial or absent. Coronoid process a high prominence but not a projecting process. Epijugal element present on jugal flange. Secondary palate extends posteriorly with inclusion of the anterior ends of the maxillae, which are in contact (Galton 1973). Vomer deep, vertically oriented sheet of bone bisecting anterior palatal vacuity. Parietal and squamosal extensively produced posteriorly, overhanging occiput. Scapula straight. Prepubis elongate. The 4th trochanter is not pendent.

While Steel (1969) commented on certain resemblances between pachycephalosaurs and ceratopsians, until this relationship is more firmly established and a monophyletic origin secured, this branch of the cladogram is unnamed.

Character suite B₁

Infraorder PACHYCEPHALOSAURIA Maryńska & Osmólska, 1974 (nom. transl.
herein *ex* suborder Pachycephalosauria)

Moderately large neornithopods with the fronto-parietal region of the skull greatly thickened and rugose, forming a dome-like prominence. Quadrate markedly inclined, with narrow lateral temporal fenestra sloping forward to beneath the orbit. Premaxilla reduced, maxilla extending up to meet the nasal. Retroarticular process well developed. Ischium decurved.

Character suite C₁

Family STENOPELIXIDAE Nopsca, 1917 (nom. correct. Kuhn, 1966)

Skull cap with two small domes, one on each frontal. Upper temporal fenestra not reduced. Frontal not excluded from orbit margin by prefrontal. Pubis reduced and excluded from acetabulum. Postpubis lacking.

The family Stenopelixidae is reintroduced because it is a senior synonym of the Pachycephalosauridae. However, since the latter taxon is based largely upon cranial material from the late Cretaceous whereas *Stenopelix* is a Weald genus, it seems prudent to retain both families pending the discovery of additional material.

Character suite D₁

Family PACHYCEPHALOSAURIDAE Sternberg, 1945

Skull cap with single dome. Upper temporal fenestrae closed or vestigial. Frontal excluded from orbit margin by fusion of prefrontal with supraorbital.

Character suite E₁

Infraorder CERATOPSIA Marsh, 1890 (nom. transl. herein
ex suborder Ceratopsia)

Upper jaw with rostral bone forming a prominent beak. Antorbital vacuities vestigial or absent. Frontals and prefrontals enter orbital border. Retroarticular process absent. Scapula of uniform width. Postpubis much reduced to obsolete. Ischium decurved.

Character suite F₁

Superfamily PSITTACOSAUROIDEA new superfamily

Premaxillary teeth lacking. Jugal deep. Lateral temporal fenestra broad. Manus with phalangeal formula 2-3-4-1-0. Sacrum with 5-6 elements. Both prepubis and postpubis short, slender. Ischium straight, long, with distal ends blade-like and united in a broad symphysis. Crest-like greater trochanter. Four distal tarsals.

Family PSITTACOSAURIDAE Osborn, 1923

Diagnosis as for superfamily.

Character suite G₁

Superfamily CERATOPSOIDEA Hay, 1902

Large-skulled quadrupeds with a cervical frill and various degrees of horn formation. Maxillary and dentary teeth set in a groove. Atlas-axis complex, together with 3rd and sometimes 4th cervical wholly or partially fused. Iliac antitrochanter prominent.

Character suite H₁

Family PROTOCERATOPSIDAE Granger & Gregory, 1923

Small ceratopsoids with at most an incipient horn core to the nasal. Postorbitals arched and rugose but without horn development. Parietal-squamosal frill short to very short. Coronoid process low. Sacrum with 6-8 elements. Ischium long, slender, almost straight.

Character suite I₁

Family CERATOPSIDAE Marsh, 1888

Large to very large ceratopsoids with large external nares situated in well-developed fossae. Cheek teeth double-rooted, up to 40 in each series. Premaxilla edentulous. Nasals broad, usually with median horn core. Frontals and prefrontals excluded from orbital border. Conspicuous posterior parietal-squamosal frill. Postorbitals greatly expanded, with horns. Sacrum with 8-11 elements. Ischium short, broad, strongly decurved. Prepubis long. The 4th trochanter is reduced. Unguals hoof-shaped.

Discussion

On the basis of the primitive characters within the above recognized clades it is possible to anticipate the ancestral ornithischian. It was a small biped with short snout, small external nares, prominent antorbital vacuities, large rounded orbits with sclerotic rings and each with a supraorbital. Dentition was heterodont and bilaterally enamelled, with simple premaxillary teeth and up to 20 compressed, single-rooted, spatulate cheek teeth. Wear surfaces were absent. The maxillary teeth closed outside those of the dentary. The nasals were narrow and there was a coronoid process. There were 24 presacrals (9 + 15), 4 sacrals and a long tail. The scapula blade broadened posteriorly and there was an acromion process. Sternal plates were present. There was a prominent deltopectoral crest to the humerus, the latter longer than the radius and ulna. The manus was relatively small and slender with digits IV and V lacking unguals, and a phalangeal formula of 2-3-4-3-2. The unguals were claw-like. The ilium was low, with a long pointed

anterior process and a shorter, broader posterior process. It possessed a supra-acetabular buttress but a brevis shelf was inconspicuous to absent. The pubis had a short prepubis and a long postpubis. The femur was sinuous with a poorly discriminated greater trochanter and a lesser trochanter adpressed to the shaft. It lacked an anterior intercondylar groove. The tibia was stout and twisted, and the hindlimbs were longer than the forelimbs. The astragalus and calcaneum were separate and there were two distal tarsals. Metatarsals II–IV were slender and elongate and the pedal phalangeal formula was 2–3–4–5–0. Digit V was vestigial and the pes was functionally tridactylous.

If the diagnostic ornithischian characters are removed from the above list, the remaining features virtually diagnose the prosauropods and support Cooper's (1981) suggestion that the Ornithischia are a neotenous offshoot of prosauropod stock. Moreover, it emphasizes the correctness of grouping the sauropodomorphs and ornithischians together in the Ornithischiformes.

SYSTEMATIC DESCRIPTION

Order ORNITHOPODA Marsh, 1871

Suborder **HYPSILOPHODONTIA** new suborder

Superfamily **HYPSILOPHODONTOIDEA** new superfamily

Family **Hypsilophodontidae** Dollo, 1882

Discussion

When the early hypsilophodonts are stacked stratigraphically it is clear that from an early stage there were a number of discrete phyletic lines. Thus, the late Kimmeridgian Morrison Formation has yielded *Othnielia*, a typical hypsilophodontid perhaps ancestral to *Hypsilophodon* itself, the primitive iguanodont *Camptosaurus*, the fabrosaurid *Nanosaurus* and the aberrant hypsilophodontid *Dryosaurus*. The coexistence of *Othnielia* and *Dryosaurus* points to an early dichotomy of the Hypsilophodontidae and the writer thus proposes:

Subfamily **Dryosaurinae** new subfamily

Diagnosis

Moderately sized hypsilophodontids with edentulous premaxillae separating maxillae and nasals. Ilium with very broad brevis shelf. Prepubis transversely flattened. Ischium with proximally situated obturator process. Femur sigmoidal, with weak to moderately developed anterior intercondylar groove, flat medial surface to inner condyle, and with insertion area for m. caudifemoralis longus well separated from 4th trochanter. Pes tridactylous, with metatarsals I and V reduced to vestigial splints.

Discussion

Were it not for the fact that *Dryosaurus* occurs side-by-side with the primitive iguanodont *Camptosaurus* it could be regarded as an ideal link between hypsilophodonts and iguanodonts. The coexistence of these two taxa points to convergence. Galton (1981) includes *Dryosaurus* within the Hypsilophodontidae, suggesting its derived characters are convergent towards the iguanodont condition. On the basis of the available evidence, the writer would also assign *Valdosaurus* and *Kangnasaurus* to this subfamily.

Genus *Kangnasaurus* Houghton, 1915

Type species *Kangnasaurus coetzeei* Houghton, 1915, by monotypy.

Kangnasaurus coetzeei Houghton, 1915

Figs 3–22

Kangnasaurus coetzeei Houghton, 1915: 19, figs 1–6. Steel, 1969: 19, fig. 8 (8–9).

Kangnasaurus . . . Lapparent & Lavocat (in Piveteau), 1955: 384. Romer, 1956: 629; 1966: 370. Thulborn, 1974: 172. Taquet, 1975: 507, fig. 3.

Holotype

By original designation, the cheek tooth, SAM–2732 (Fig. 3).

Hypodigm

In addition to the holotype, the following material was collected from the same well and in large part was used to supplement the original description of *K. coetzeei*:

SAM–2731 — right femur

2731a — proximal end of right femur

2731b — distal end of right femur

2731c — distal end of left femur

2731d — proximal end of right femur

2731e — articulated distal left femur and proximal portion of tibia

2731f — four articulated caudal vertebrae

2731g — distal end of left metatarsal

2731h — ?

2731i — ?

2731j — distal portion of right tibia with articulated tarsus and proximal portion of metatarsus

Locality

Rogers (1915) gave the locality as a well on the farm Kangnas, ' . . . in a wide shallow valley leading to the Orange River at Henkries'. The well from which *Kangnasaurus* was obtained was sunk in the Koa River valley, about 7.5 km south of Henkries Mond in Little Bushmanland, and 15 km south-west of Goodhouse (Fig. 1).

Description

Tooth

A single cheek tooth is the only cranial fragment available (Fig. 3). It was identified by Haughton (1915) as a right maxillary tooth but in *hypsilophodontids* it is the dentary teeth that bear a strong median keel. The tooth is enamelled on both surfaces, spatulate, and without a cingulum or constriction between root and crown. The root seems to have been long and tapering, implying a fairly deep dentary, with a subhexagonal cross-section and oval pulp cavity. The crown is longitudinally curved and with a subrhomboidal medio-lateral profile. The convex surface is strongly ridged, with a median keel forming a distinct spike to the cutting edge, as in *Hypsilophodon*. In addition, there are strong ridges along both the anterior and posterior margins, the stronger of which was believed by Haughton (1915) to be the posterior one. Between these main ridges are a number of slightly diverging subsidiary ridges, six on one side of the median keel and eight on the other. The concave surface shows very faint and indistinct longitudinal ridging and a pronounced biconcave wear facet indicating occlusion with two teeth of the opposite jaw during mastication. Thus the maxillary and dentary tooth rows were parasagittally offset, relative to one another. The cutting edge of the crown is weakly serrated by the subsidiary ridges on the convex surface.

Cervical vertebra

A single fragment of a cervical centrum (Fig. 4) gives the impression of having been relatively long and strongly waisted at midlength, with a prominent ventral keel. The articular face is convex, with a distinct pit just below centre. It seems likely that this centrum was opisthocoelous, as in *Camptosaurus* and *Hypsilophodon*.

Dorsal vertebra

A beautifully preserved dorsal centrum is platycoelous, almost amphiplatyan, with suboval anterior and posterior profiles (Fig. 5). Viewed laterally both the anterior and posterior rims are broadly scarred for muscle attachment, and there is a small nutritive foramen. Ventrally the centrum is narrowly rounded. The ventral surface of the neural canal is pierced by a prominent, elongate foramen, similar to but not as elongate as that of *Dryosaurus lettowvorbecki* (Virchow) (Janensch 1955, fig. 22a).

Caudal vertebrae

There are six caudal vertebrae in the available material (Figs 6–8), four of which comprise an articulated series. The largest is an isolated centrum (Fig. 6) showing a subhexagonal cross-section at midlength, with the ventral surface weakly grooved posteriorly. Three tiny foramina pierce the ventral surface and there are distinct facets for chevron articulation posteriorly. In lateral view the



Fig. 3. *Kangnasaurus coetzeei* Houghton. The holotype, SAM-2732, an alleged maxillary tooth. A. Labial view. B. Lingual view. C. Anterior view. Note the biconcave occlusal wear surface. Bar scale = 5 mm.

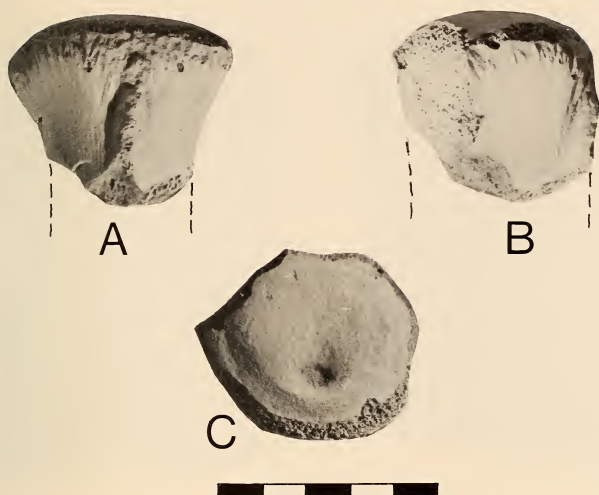


Fig. 4. *Kangnasaurus coetzeei* Haughton. Fragment of a cervical vertebra. A. Ventral view. B. Lateral view. C. Anterior view. Note the prominent ventral keel. Bar scale = 25 mm.

anterior and posterior rims of the centrum are strongly scarred, while there is a weak horizontal ridge at about midflank. The ventral surface of the neural canal is perforated by two small foramina at about midlength.

The articulated series (Fig. 7) lacks transverse processes and the neural spines are very reduced. Since transverse processes are not lost before the twelfth vertebra in *Camptosaurus* (Galton & Powell 1980) and *Dryosaurus* (Galton 1981), they are from the mid-portion of the series. The neurocentral sutures are obsolete, their approximate positions marked by horizontal ridges. The lateral surfaces of the centra are slightly concave while the ventral surface is weakly grooved, giving the centra hexagonal cross-sections at midlength. There are distinct chevron facets. The prezygapophyses are short, with subvertical articular facets, and only just protrude beyond the anterior border of the centrum. The postzygapophyses are naturally much longer, distinctly ridged and grooved (Fig. 7), while there are two shallow dimples on the dorsal surface of the neural arch, just behind the prezygapophyses, a feature also seen in the prosauropod *Massospondylus* (Cooper 1981, fig. 15C).

Ribs

A proximal fragment of an anterior dorsal rib (Fig. 9) is the only bone showing any features of note. The capitular pedicel and capitulum are broken off,

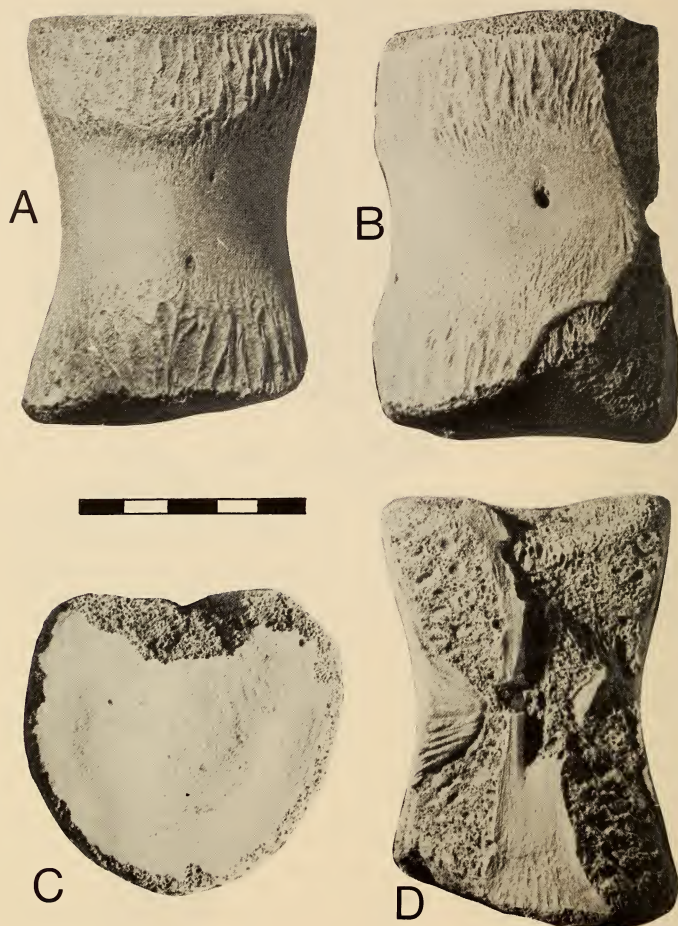


Fig 5. *Kangnasaurus coetzeei* Haughton. A dorsal centrum. A. Ventral view. B. Lateral view. C. Anterior view. D. Dorsal view. Bar scale = 25 mm.

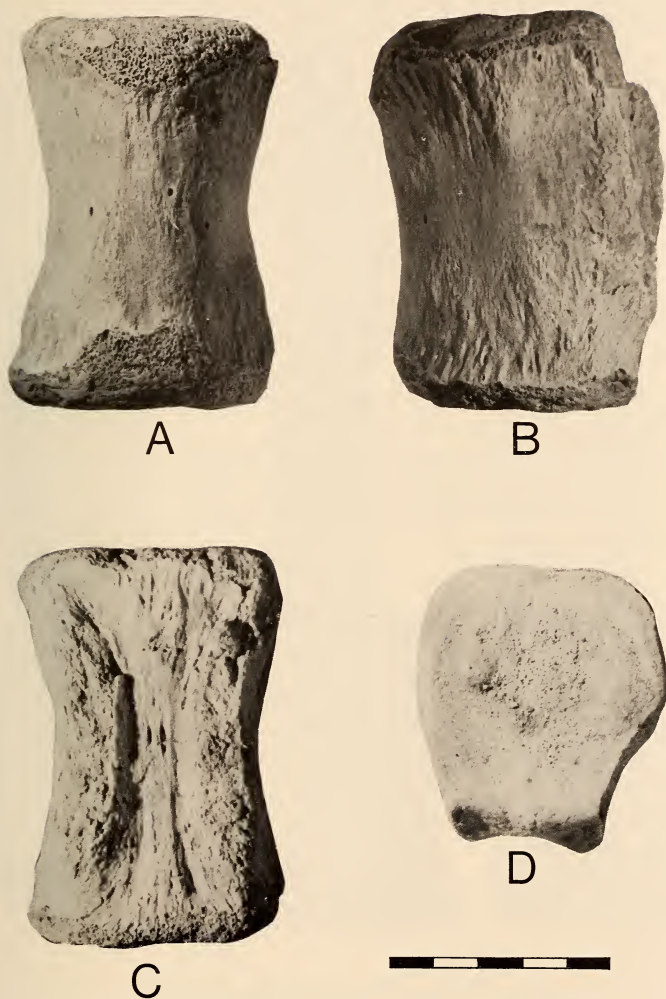


Fig. 6. *Kangnasaurus coetzeei* Haughton. A mid-caudal centrum. A. Ventral view. B. Lateral view. C. Dorsal view. D. Posterior view. Bar scale = 25 mm.

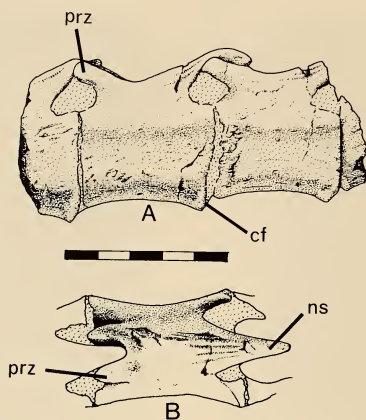


Fig. 7. *Kangnasaurus coetzeei* Haughton. Articulated mid-caudal vertebrae, SAM-2731f. A. Lateral view. B. Dorsal view. Note the longitudinally grooved neural spines and sub-pentagonal centra. Bar scale = 25 mm.

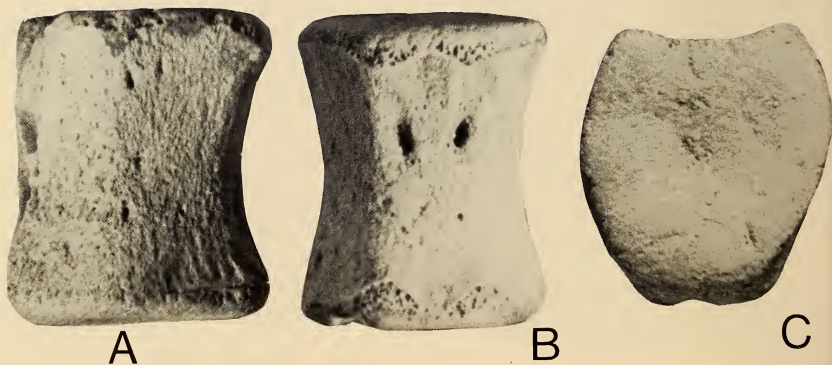


Fig. 8. *Kangnasaurus coetzeei* Haughton. A posterior caudal centrum. A. Lateral view. B. Ventral view. C. Posterior view. Bar scale = 10 mm.



Fig. 9. *Kangnasaurus coetzeei* Haughton. Fragment of an anterior dorsal rib. A. Anterior view. B. Ventral view. C. Posterior view. Bar scale = 25 mm.

but there is a short tubercular pedicel with an elliptical tuberculum. Immediately lateral to the tuberculum the rib has a V-shaped cross-section, with the apex situated in the middle of the anterior surface. However, the anterior ridge quickly shifts to an anteroventral position when the ventral surface of the rib becomes gently concave.

Manus

A peculiar bean-shaped bone (Fig. 10) may be a manual phalanx or metacarpal V. It is distinctly asymmetrical, dorsoventrally flattened, and with rounded proximal and distal articular surfaces.

Pelvis

What may be a fragment of the proximal plate of an ischium is the only pelvic remnant available. However, it is too scrappy and poorly preserved for proper identification or description.



Fig. 10. *Kangnasaurus coetzeei* Haughton. Bone tentatively identified as metacarpal V. A. Anconal view. B. Lateral view. Bar scale = 10 mm.

Femur

The characters of the femur are well displayed by several specimens (Figs 11–17). The femur is rather gracile (length/minimum transverse width = 8.75), sigmodially curved in medial view (Fig. 12A) and strongly expanded at both ends. The greater trochanter accounts for the proximal parasagittal expansion and shows a gently curved dorsal surface in lateral view (Fig. 12B). The lesser trochanter is closely adpressed to the greater trochanter, as in *Hypsilophodon*, and not separated from it by a deep cleft as in *Valdosaurus*, *Dryosaurus*, *Camptosaurus*, *Callovosaurus* and other ornithopods. There is some

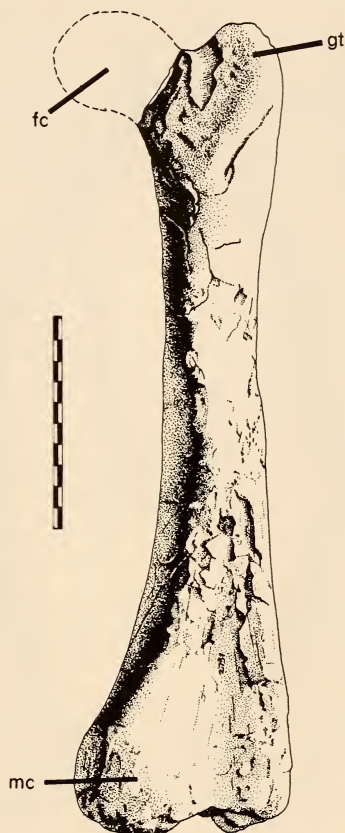


Fig. 11. *Kangnasaurus coetzeei* Haughton.
A right femur, SAM-2731, anterior view.
Drawing reversed. Bar scale = 100 mm.

variation in the dorsal extent of the lesser trochanter. It is well below the level of the greater trochanter in SAM-2731 (Fig. 12), but only slightly so in SAM-2731a (Fig. 14). The 4th trochanter is not preserved in any of the available material, although SAM-2731 (Fig. 12) shows it to have been broad-based and with its distal termination situated at midlength. It is likely to have been produced posteriorly into a pendent, acuminate flange. The depression for the insertion of

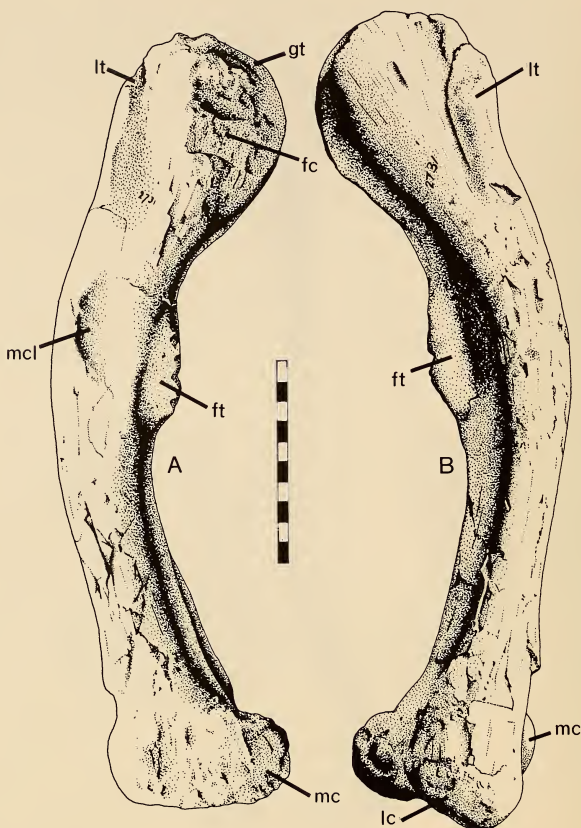


Fig. 12. *Kangnasaurus coetzeei* Houghton. A right femur, SAM-2731. A. Medial view. B. Lateral view. See also Fig. 11. Bar scale = 100 mm.

m. caudifemoralis longus is well separated from the 4th trochanter, in a comparable position to *Dryosaurus* (cf. Galton 1981, fig. 14C, I). Distally there is a moderately developed anterior intercondylar groove (Figs 13, 16), comparable to the condition in some individuals of *Dryosaurus* (cf. Galton 1981, fig. 14J, L). The distal end of the femur is strongly expanded transversely, with a very large inner condyle and a smaller lateral condyle. As in *Dryosaurus* and *Hypsi-
lophodon* the medial surface of the inner condyle is flat. In the popliteal space

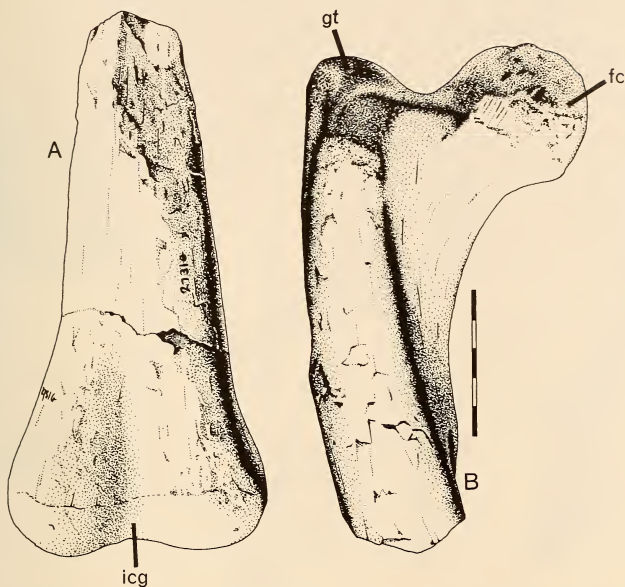


Fig. 13. *Kangnasaurus coetzeei* Haughton. A. Distal end of a left femur, SAM-2731c, anterior view. B. Anterior view of the proximal head of a right femur, SAM-2731a. Bar scale = 50 mm.

between the inner and outer condyles of SAM-2731b (Fig. 15) is a rugose area that marks the insertion of musculature referred to aponeurosis 1 in birds and the prosauropod *Massospondylus* (Cooper 1981, fig. 84). Proximally the femoral head is well developed, with a swollen rounded condyle, which is separated dorsally from the greater trochanter by a pronounced groove (Fig. 17). The posterior surface of the femoral condyle is distinctly concave, forming a posteromedial lip.

Tibia

A complete tibia is unknown, only the proximal and distal ends being preserved. SAM-2731e comprises the distal end of a left femur articulated to the proximal end of a tibia (Fig. 18A–B). The proximal head is strongly expanded, with a well-developed cnemial crest that curves markedly outwards and is separated from the accessory condyle by a broadly concave groove. Posteriorly, the proximal articular surface shows well-developed inner and outer condyles, the former the more prominent of the two. There is a pronounced accessory condyle

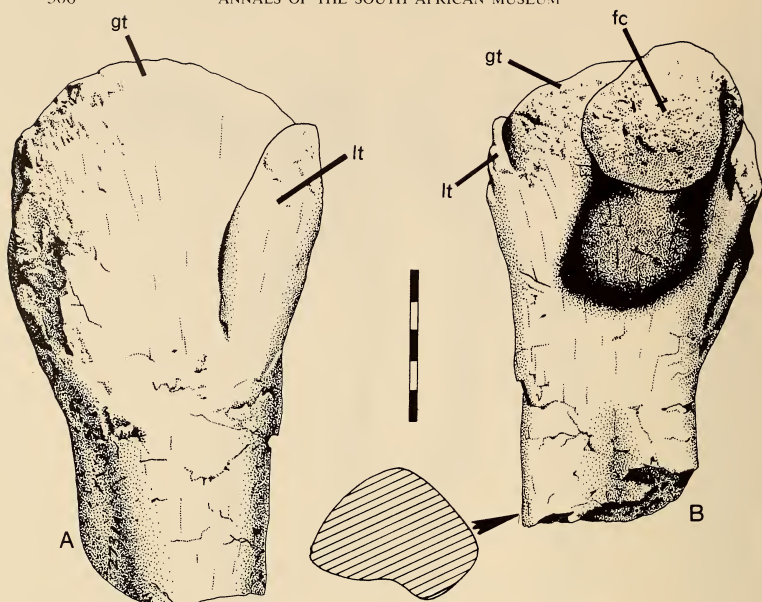


Fig. 14. *Kangnasaurus coetzeei* Haughton. Proximal head of a right femur, SAM-2731a. A. Lateral view. B. Medial view. Note how the lesser trochanter does not reach the level of the greater trochanter. See also Fig. 12B. Bar scale = 50 mm.

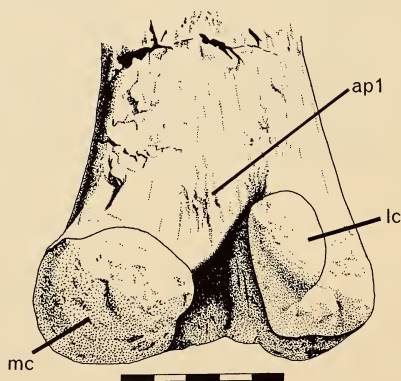


Fig. 15. *Kangnasaurus coetzeei* Haughton. Distal end of a right femur, SAM-2731b, in posterior view. Bar scale = 50 mm.

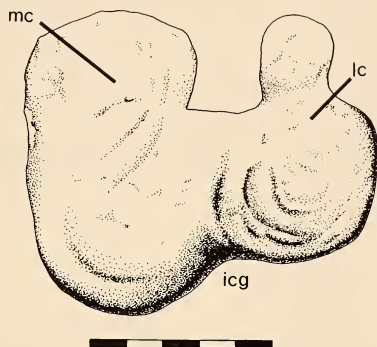


Fig. 16. *Kangnasaurus coetzeei* Haughton. Distal articular surface of a right femur, SAM-2731b. Bar scale = 50 mm.

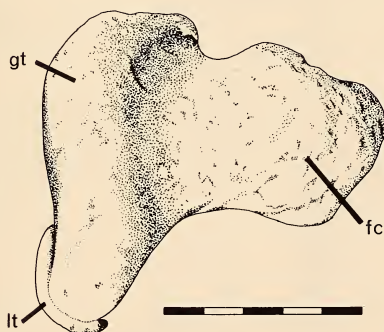


Fig. 17. *Kangnasaurus coetzeei* Haughton. Proximal view of a right femur, SAM-2731a. Note lack of a broad cleft separating lesser and greater trochanters. Bar scale = 50 mm.

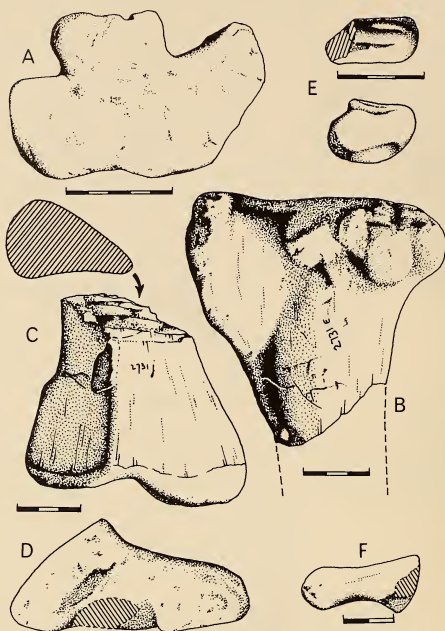


Fig. 18. *Kangnasaurus coetzeei* Haughton. A-B. Proximal articular surface and lateral view of the proximal head of a right tibia, SAM-2731e. C. Distal end of a right tibia, SAM-2731j, in posterior view, with a cross-section of the shaft. D. Distal articular surface of a right tibia, SAM-2731j. E. Anconal and posterior views of distal tarsal IV of the right pes, SAM-2731j. F. Palmar? view of metatarsal V of the right pes of SAM-2731j. Bar scales in 5 mm divisions.

on the lateral surface of the outer condyle for articulation with the fibula, as in *Dryosaurus* (Galton 1981, figs 16A, E-F, 19K) and *Hypsilophodon* (Galton 1974a, fig. 56A, E). Distally the preserved portion of SAM-2731e tapers rapidly and shows a suboval cross-section. SAM-2731j comprises the distal end of a right tibia, together with loosely articulated tarsus and the proximal ends of the metatarsals. The tibial fragment (Fig. 18C-D) is similar to both *Hypsilophodon* (Galton 1974a, fig. 56) and *Camptosaurus* (Galton & Powell 1980, fig. 10L). It is not significantly different from those tibiae of *Dryosaurus* in which a posterior notch for the reception of the astragalus is lacking (Galton 1981). The anterior

surface of the outer malleolus is flat, for apposition with the distal end of the fibula. The distal end of the tibia tapers proximally into a subtrigonal, anteroposteriorly compressed shaft.

Astragalus

The astragalus is a thin cup of bone (Fig. 19D) which fitted snugly against the distal end of the tibia. Its cupped dorsal surface is shallowly biconcave, with the lateral cotylus the larger of the two. The distal roller is not completely exposed but seems to have been smooth and weakly biconvex, with a shallow median groove.

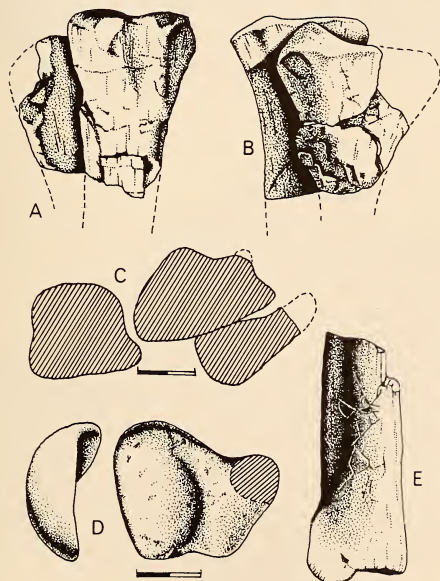


Fig. 19. *Kangnasaurus coetzeei* Haughton.
A-B. Right metatarsals III and IV of SAM-2731j in anconal and palmar views. C. Proximal profiles of right metatarsals II-IV of SAM-2731j. E. Medial view of proximal end of metatarsal II of SAM-2731j.
Bar scales in 5 mm divisions.

Calcaneum

The calcaneum (Figs 20–21) is closely comparable to those of *Hypsilophodon* (Galton 1974a, fig. 57A–E), *Camptosaurus* (Galton & Powell 1980, fig. 11F–G) and *Dryosaurus* (Galton 1981, fig. 15A–C). The lateral surface is slightly concave, almost flat, faintly scarred, and with a weak anteroventral rim which is interrupted for a short distance ventrally. There is also a very weak dorsal rim, just below the fibular facet. The most conspicuous feature of the medial surface is a prominent tubercle, above which are four foramina. The distal roller is semi-circular, smooth, and faintly corrugated, while the fibular facet is gently concave and the tibial facet strongly concave.

Distal tarsals

A single distal tarsal (Fig. 18E) is preserved, which, to judge from its form and position within the tarsus, is distal tarsal IV. Its medial edge is broken, but it seems to have formed an elongate hemicylinder. The anterior surface bears two deep grooves for ligament attachment, the dorsal surface is flat, the ventral surface smoothly rounded for articulation with metatarsal IV, and the posterior surface is shallowly concave.

Metatarsus

Apparently there were only four metatarsals to the pes of *Kangnasaurus*, there being no evidence for metatarsal I; presumably it was obsolete. Metatarsals II–IV are known only from their proximal ends. That of metatarsal II is not well preserved but had a narrowly ovate proximal articular surface (Fig. 19C) whose long axis seems to have been oriented subvertically. The proximal articular surface of metatarsal III has an irregular profile, unlike that of any other hypsilophodontid, while that of metatarsal IV is almost square but with a depression on the lateral half of the surface for reception of distal tarsal IV. The palmar surface of metatarsal IV is also deeply excavated to receive the vestigial metatarsal V (Fig. 18F). The latter is a thin, narrow strap of bone, slightly curved along its length, and similar in form and position to that of *Dryosaurus* (cf. Galton 1981, fig. 15H).

Phalanges

The only pedal phalanx available is an asymmetrical, dorsoventrally compressed ungual (Fig. 22) with deep medial and lateral grooves. The asymmetry suggests it is from the right foot. It is non-diagnostic, but indistinguishable from those of *Dryosaurus* and *Camptosaurus*.

Discussion

It is clear from the foregoing description of the known elements of *Kangnasaurus* that it is a distinctive ornithopod, most closely allied to the *Dryosaurus*–*Hypsilophodon* plexus. As such, its previous interpretation as an iguanodontid (Lapparent & Lavocat in Piveteau 1955; Romer 1956, 1966; Steel



Fig. 20. *Kangnasaurus coetzeei* Haughton. Left calcaneum. A. Lateral view. B. Medial view. Bar scale = 10 mm.



Fig. 21. *Kangnasaurus coetzeei* Haughton. A. Anterior view. B. Posterior view. Note the pronounced median 'tubercle'. Bar scale = 10 mm.



Fig. 22. *Kangnasaurus coetzeei* Haughton. Right pedal ungual. A. Lateral view. B. Anconal view. Bar scale = 25 mm.

1969; Thulborn 1974; Taquet 1975) is incorrect (a conclusion independently reached by P. M. Galton, *in litt.*, 1981).

Kangnasaurus is readily distinguishable from *Iguanodon* (Hooley 1925) by its more gracile construction, sigmoidal femur with a shallow anterior intercondylar groove, and markedly different cheek teeth. *Callovosaurus* is based upon a femur (Galton 1980) whose greater trochanter does not show the parasagittal expansion seen in *Kangnasaurus*, while its lesser trochanter is expanded transversely and separated from the greater trochanter by a deep cleft.

The camptosaurid *Muttaburrasaurus* (Bartholomai & Molnar 1981) has a much more robust femur than *Kangnasaurus*, with a distinctly smaller lesser trochanter and a greater trochanter that does not show the parasagittal expansion of *Kangnasaurus*. Its maxillary teeth are also rather different with up to 13 fine, subparallel ridges on the labial surface, all of comparable strength.

Kangnasaurus differs from *Camptosaurus* (Galton & Powell 1980) in the presence of an accessory (fibular) condyle to the tibia, a generally more sigmoidal and less robust femur, and in having its lesser trochanter closely adpressed to the greater trochanter.

Thescelosaurus (Parks 1926; Galton 1974b; Morris 1976) is a hypsilophodontid that has a much more robust femur than the South African genus, with the 4th trochanter extending on to a distal half of the shaft. In addition it has a relatively well-developed first pedal digit and a peculiar ankle arrangement (Morris 1976), in some species at least.

In its closely adpressed lesser and greater trochanters and flat medial surface to the inner femoral condyle, *Kangnasaurus* is very similar to *Hypsilophodon* and both show 'high-spiked' dentary teeth. *Hypsilophodon*, however, differs in lacking an anterior intercondylar groove to the femur, the greater trochanter does